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Ocean Acidification and Coral Reefs: Effects on Breakdown, Dissolution, and Net Ecosystem Calcification

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Abstract

The persistence of carbonate structures on coral reefs is essential in providing habitats for a large number of species and maintaining the extraordinary biodiversity associated with these ecosystems. As a consequence of ocean acidification (OA), the ability of marine calcifiers to produce calcium carbonate (CaCO₃) and their rate of CaCO₃ production could decrease while rates of bioerosion and CaCO₃ dissolution could increase, resulting in a transition from a condition of net accretion to one of net erosion. This would have negative consequences for the role and function of coral reefs and the eco-services they provide to dependent human communities. In this article, we review estimates of bioerosion, CaCO₃ dissolution, and net ecosystem calcification (NEC) and how these processes will change in response to OA. Furthermore, we critically evaluate the observed relationships between NEC and seawater aragonite saturation state (Ω_a). Finally, we propose that standardized NEC rates combined with observed changes in the ratios of dissolved inorganic carbon to total alkalinity owing to net reef metabolism may provide a biogeochemical tool to monitor the effects of OA in coral reef environments.

Ocean acidification (OA): addition of CO_2 in seawater that causes a reduction in seawater pH and carbonate saturation state (Ω)

Net ecosystem calcification (NEC): total calcification minus total CaCO_3 dissolution; historically, it has also been referred to as G or g

INTRODUCTION

Ocean acidification (OA) has raised concerns about its effects on marine organisms and ecosystems, particularly for those reliant on the generation and accumulation of calcium carbonate (CaCO_3) shells, tests, skeletons, and/or structures. The persistence of shallow coral reef ecosystems is ultimately dependent upon the system having a carbonate mass balance budget in which the constructive processes [i.e., the biomineralization, calcification, and formation of CaCO_3 (gain)] exceed or are equal to the destructive processes [i.e., the breakdown, export, and dissolution of CaCO_3 sediments and substrates (loss)] (e.g., Hutchings 1986; Glynn 1997; Kleypas et al. 1999a, 2001; Kleypas & Langdon 2006; Erez et al. 2011). The buildup and maintenance of complex carbonate structures on coral reefs are essential in providing habitats for a large number of species and maintaining the high biodiversity associated with these ecosystems. Carbonate production also provides direct eco-services to human coastal communities by replenishing beaches and mitigating potentially destructive wave energy from storms or tsunamis.

As a consequence of OA, the rate of CaCO_3 production of marine calcifiers on coral reefs may significantly decrease (e.g., Gattuso et al. 1999, Kleypas et al. 1999a, Langdon et al. 2003, Marubini et al. 2003, Schneider & Erez 2006, Andersson et al. 2011, Erez et al. 2011) while rates of bioerosion and CaCO_3 dissolution could increase (Andersson et al. 2003, 2005, 2009; Morse et al. 2006; Tribollet et al. 2009; Tynan & Opdyke 2011). Additionally, should the frequency and intensity of coral bleaching events and storms increase in a warmer world, there will be an increasing loss of CaCO_3 from coral reefs through physical breakdown and export (e.g., Glynn 1991, Hoegh-Guldberg et al. 2007, Baker et al. 2008, Pandolfi et al. 2011). Consequently, concerns have been raised that OA and climate change could cause coral reefs to transition from a condition of net CaCO_3 accretion to one of net erosion, which would have drastic consequences for their role and function as ecosystems (Andersson et al. 2005, 2009; Hoegh-Guldberg 2005; Hoegh-Guldberg et al. 2007; Silverman et al. 2009).

There remains considerable uncertainty about when the geochemical threshold at which net accretion shifts to net erosion might be crossed with respect to atmospheric or seawater CO_2 levels as inferred from mesocosm experiments, field experiments, and modeling simulations at both the local and global scales (e.g., Yates & Halley 2003, 2006; Andersson et al. 2005, 2009; Hoegh-Guldberg et al. 2007; Silverman et al. 2009). Although some of this uncertainty reflects differences between reef environments (e.g., physiochemical setting), community composition, and local biogeochemistry, there also remains much uncertainty in estimating past and contemporary rates of net ecosystem calcification (NEC), let alone predicting how these rates will change in response to future OA and climate change. Identifying the timing and chemical threshold when $\text{NEC} = 0$ for different coral reef systems in response to OA and climate change is of great relevance, representing a physical tipping point where CaCO_3 loss exceeds gain and the persistence of coral reefs can no longer be sustained. The timing of this tipping point will vary across different reef environments, thus dividing them into systems more or less at risk.

Most of the experimental and observational research to date on the implications of OA for coral reefs has focused on its effect on the production and growth rates of calcareous hard parts by marine organisms and communities; considerably less attention has been given to its effect on destructive processes such as bioerosion and CaCO_3 dissolution. To accurately forecast and predict the effect of OA on coral reef CaCO_3 budgets, it is equally important to understand the effect on calcification and on bioerosion and CaCO_3 sediment dissolution.

One plausible approach to estimating the timing of the geochemical threshold when $\text{NEC} = 0$ on coral reefs would be to derive it from reliably quantified NEC rates across a natural range of seawater carbonate chemistry. In fact, several field and experimental studies have made



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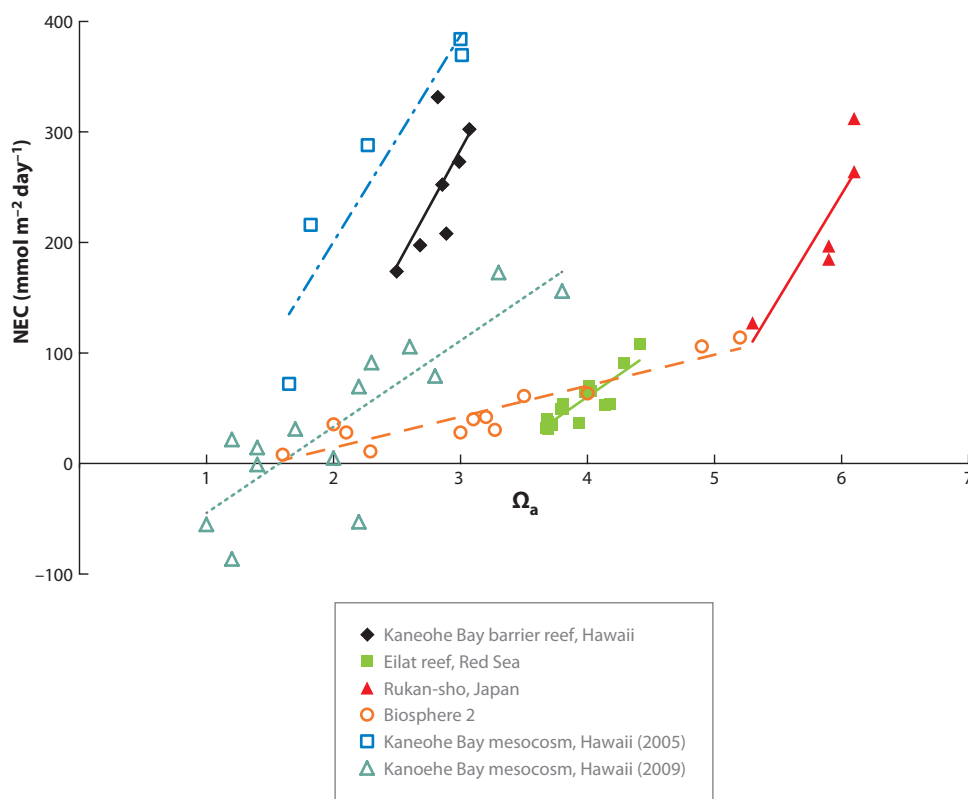


Figure 1

Net ecosystem calcification (NEC) rate as a function of seawater aragonite saturation state (Ω_a). Adapted from Shamberger et al. (2011) with permission from Elsevier.

such attempts, and generally tend to reveal a strong correlation between NEC rates and seawater aragonite saturation state (Ω_a) (e.g., Boucher et al. 1998; Ohde & van Woesik 1999; Langdon et al. 2000, 2003; Leclercq et al. 2000, 2002; Silverman et al. 2007a,b, 2009; Andersson et al. 2009; Shamberger et al. 2011). Most studies have reported decreasing NEC rates with decreasing seawater Ω_a , which could be described through a simple regression analysis whereby the intercept represents the threshold at which calcification equals dissolution (i.e., $\text{NEC} = 0$). However, the intercept and slope of these observed relationships between NEC and Ω_a vary greatly across locations and investigations (Figure 1).

To better understand how coral reef NEC will be affected by OA and decreasing seawater Ω_a , it is critical to understand why the relationships between NEC and Ω_a in prior studies differ. We find that NEC rates might prove more interpretable when other concomitant processes such as net ecosystem production (NEP)—which can strongly impact the local balance of dissolved inorganic carbon (DIC) to total alkalinity (TA), and hence Ω_a —are considered. This may help to resolve some of the previous disparities between the measured NEC- Ω_a relationships and potentially offers a valuable biogeochemical monitoring tool for tracking the long-term effects of OA and climate change on coral reef performance and function.

Aragonite: CaCO_3 with an orthorhombic mineral structure, the mineral phase deposited by corals

Net ecosystem production (NEP): total primary production minus total autotrophic and heterotrophic respiration

Dissolved inorganic carbon (DIC): the sum of aqueous CO_2 , carbonic acid, bicarbonate, and carbonate ions

Total alkalinity (TA):

the difference between major cations and anions, equivalent to the excess of proton acceptors over proton donors in 1 kg of seawater

Seawater CaCO_3 saturation state (Ω):

thermodynamic index indicating the anticipated net direction of the reaction $\text{CaCO}_3 \rightleftharpoons \text{Ca}^{2+} + \text{CO}_3^{2-}$; supersaturation ($\Omega > 1$) favors CaCO_3 formation, whereas undersaturation ($\Omega < 1$) favors dissolution

CONSTRUCTION OF CORAL REEFS

Calcification is the process of combining calcium (Ca^{2+}) and carbonate (CO_3^{2-}) ions to form the mineral CaCO_3 . When this process is biologically facilitated, it is best termed biocalcification and occurs at rates orders of magnitude faster than those of inorganic CaCO_3 precipitation. The origin of the biocalcification process in marine organisms is debated, but one hypothesis suggests that it arose as a detoxification mechanism under seawater conditions with $[\text{Ca}^{2+}]$ much higher than that of the present time (Brennan et al. 2004). The real explanation may be much more complex, but regardless of the origin, organisms depositing shells, tests, and skeletons made of CaCO_3 gain a range of benefits, including structural support, protection from predators, increased surface area, and mechanisms to maintain elevation above the sediment-water interface, maintain close proximity to high light levels, and keep up with sea level rise. From a geological perspective, keeping up with sea level rise is an absolute requirement for the long-term persistence of coral reef ecosystems.

The current distributions of coral reefs and carbonate platforms are in part a consequence of the rise in sea level and flooding of the continental shelves that have taken place since the Last Glacial Maximum (from approximately 22,000 years ago until the present). Because of the increases in space and shallow surface areas with high light levels, CaCO_3 deposition in the coastal environment has significantly increased during this period (Milliman 1993, Milliman & Droxler 1996, Kleypas 1997, Vecsei & Berger 2004). Based on numerical model simulations, Kleypas (1997) estimated that the coral reef area and CaCO_3 production during the Last Glacial Maximum were restricted to 20% and 27% of the current area and production, respectively. Estimates suggest that more CaCO_3 is currently being deposited in marine sediments than can be compensated for through Ca^{2+} input to the ocean via rivers and hydrothermal sources, and thus the oceanic CaCO_3 budget is currently in a nonsteady state (Milliman 1993, Milliman & Droxler 1996). Approximately 50% of all CaCO_3 that accumulates in marine sediments is stored in shallow coastal and shelf environments, and almost half of this amount accumulates in coral reef environments (Milliman 1993, Milliman & Droxler 1996).

Most of the CaCO_3 production on coral reefs is attributed to corals and various calcifying algae, but the relative contributions vary. In some reef systems, CaCO_3 production by algae is more important than calcification by corals; these reefs are perhaps best described as coralgal reefs (e.g., Vroom et al. 2006, Vroom 2011). Coral and algal growth rates vary across species, locations, environments, and seasons. Light is probably the most important parameter controlling calcification and growth rates in hermatypic corals, but temperature, food and nutrients, hydrographic regime, and seawater CO_2 chemistry [e.g., CO_2 , H^+ , HCO_3^- , CO_3^{2-} , and CaCO_3 saturation state (Ω)] are also important variables directly affecting coral calcification and growth rates (e.g., Kleypas et al. 1999b, 2001). The growth rates of individual coral colonies range from a few millimeters to a few centimeters per year for massive colonies and can be up to several centimeters per year for faster-growing branching colonies (e.g., Buddemeier et al. 1974, Hudson 1981, Lough & Barnes 1997). In terms of calcification and CaCO_3 production, individual corals typically deposit 0.5–3.0 g $\text{CaCO}_3 \text{ cm}^{-2} \text{ year}^{-1}$ (e.g., Lough & Barnes 1997, Bessat & Buigues 2001), whereas on a reef area basis, calcification by corals and algae contributes 1,500–10,000 g $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Smith & Kinsey 1976, Kinsey 1985, Milliman 1993).

The calcification rates of calcifying algae can be high: The green alga *Halimeda* is able to generate as much as 2,000–4,000 g $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Rees et al. 2007), and crustose coralline algae reportedly have the potential to generate 1,500–10,300 kg $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$, assuming 100% cover (Chisholm 2000). Crustose coralline algae also serve other important functions and roles on coral reefs by acting as the glue or cement of the reef surface and releasing chemical



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compounds into the water column that serve as settlement cues for coral larvae (Morse et al. 1996). Coral reefs host many other calcifying organisms that contribute to CaCO_3 production, including benthic foraminifera, echinoderms, molluscs, and bryozoans. Their contributions to the CaCO_3 budget can be highly significant at the local scale—e.g., estimates for benthic foraminifera range from 150 to 2,800 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Hallock 1981)—but are probably relatively small compared with the overall contribution from corals and calcifying algae. The majority of a coral reef is made up not of coral framework but rather of sedimentary environments comprising CaCO_3 particles and substrates produced by destructive physical and biological processes (Hutchings 1986, Glynn 1997). Based on the average sediment composition of shallow subtropical and tropical environments (Chave 1967, Morse et al. 2006), these sediments are typically composed of ~60% aragonite, ~25% Mg calcite, and ~15% calcite/low-Mg calcite. The growth rates of coral reefs vary within reefs, between reefs and geographical locations, and across time. Estimates range from 0.2 to 16 m per thousand years (see summary in Rees et al. 2007).

PHYSICAL, CHEMICAL, AND BIOLOGICAL BREAKDOWN AND DISSOLUTION OF CORAL REEFS

The erosion and breakdown of coral reefs are governed by interrelated physical, biological, and chemical processes. Currents and waves constantly erode and shape the reef structure over long periods. In contrast, large waves and major storms can rapidly cause severe structural damage to coral reefs and export large quantities of CaCO_3 sediments to deeper water. Biological and chemical erosion facilitates physical breakdown by weakening reef structures through mechanical abrasion and dissolution. In turn, the physical breakdown of CaCO_3 structures and substrates to smaller sizes can further promote the biological and chemical dissolution because of the resulting increase in the ratio of surface area to volume. Conversely, it may also be the case that this breakdown facilitates inorganic precipitation on the surfaces of these substrates, as they can serve as nucleation sites in seawater supersaturated with respect to a particular CaCO_3 mineral phase.

The magnitude of CaCO_3 dissolution and export from coral reefs is poorly quantified; similarly, we know little about the relative contributions of different bioerosion and dissolution processes. On a global scale, current estimates suggest that coral reefs produce 0.9 Pg $\text{CaCO}_3 \text{ year}^{-1}$, of which 0.7 Pg accumulates within reef areas (Milliman 1993, Milliman & Droxler 1996, Iglesias-Rodriguez et al. 2002) and the remaining 0.2 Pg is either exported or dissolved. But these are rough estimates, and we have a poor understanding of the relative magnitudes of these different pathways.

Environmental and Metabolic Dissolution of CaCO_3

Chemical dissolution can be separated into two categories: environmental dissolution and metabolic dissolution. The former refers to the dissolution of CaCO_3 substrate immersed in seawater undersaturated with respect to a particular mineral phase (i.e., $\Omega < 1$). Present-day tropical and subtropical coral reefs are immersed in surface seawater well supersaturated with respect to calcite and aragonite, and will remain supersaturated with respect to these mineral phases even in the worst-case CO_2 emission scenario (Andersson et al. 2005, 2006). Hence, the environmental dissolution of these mineral phases is unlikely except in special cases where, for example, river and groundwater inflow or upwelling may cause significant seawater undersaturation with respect to these phases. However, a significant fraction of the carbonate material on coral reefs is composed of Mg calcite, which (depending upon its mole fraction of Mg) can be more soluble than calcite and aragonite. Some of these mineral phases may exist close to a metastable equilibrium with

Calcite: CaCO_3 with a rhombohedral mineral structure, the least soluble of the commonly occurring carbonate mineral phases

Mg calcite: calcite in which 2–30 mol% of the calcium ions have been randomly replaced by magnesium ions, distorting the ideal mineral structure and causing it to exhibit a broad range of solubilities

Metastable: term describing a mineral phase that is technically in a state of disequilibrium based on thermodynamic principles but that persists because of kinetic constraints

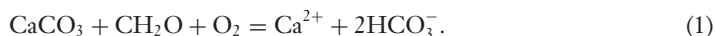


Microenvironment:

a small specific area isolated from its immediate surroundings, e.g., inside particle and organic matter aggregates, sediments, or a reef matrix

seawater that could become undersaturated owing to small changes in seawater CO₂ chemistry (Andersson et al. 2008).

Even though coral reef environments are immersed in surface seawater supersaturated with respect to the commonly occurring carbonate phases, seawater undersaturation with respect to these mineral phases can be generated in microenvironments within the reef matrix and in sediment pore waters owing to the microbial remineralization of organic material that produces CO₂ and drives dissolution. This process is commonly referred to as metabolic dissolution (e.g., Emerson & Bender 1981, Archer et al. 1989, Walter & Burton 1990, Hales et al. 1994, Hales & Emerson 1996, Jahnke & Jahnke 2004, Burdige et al. 2010, Mackenzie & Andersson 2011). The extent of dissolution is directly linked to the amount of organic material being remineralized, which can be expressed by the equation



Evidence of metabolic dissolution under aerobic conditions can be demonstrated by a property-property plot of DIC as a function of TA that has a slope close to 1 (Moulin et al. 1985, Morse & Mackenzie 1990, Burdige et al. 2008, Mackenzie & Andersson 2011). Because of the link to the extent of organic matter decay, metabolic CaCO₃ dissolution is obviously related to the amount of organic matter, its reactivity, and the rate at which it is remineralized. The remineralization rate is linked to the supply of oxygen, which most often becomes the limiting factor in sediment pore waters and microenvironments. As oxygen becomes scarce and microbes turn to alternative electron acceptors, the pore water carbonate saturation state may subsequently increase owing to increasing TA.

For example, this process occurs in the case of sulfate reduction and the accompanying deposition of FeS, which drives up TA and can actually result in the precipitation of CaCO₃. However, this process can be complex, as excess H⁺ generated in the initial stages can conversely drive CaCO₃ dissolution, particularly in Fe-poor sediments (Morse & Mackenzie 1990, Walter & Burton 1990, Tribble 1993, Walter et al. 1993, Ku et al. 1999). Bioturbation, bioirrigation, and advection of water are additional important mechanisms that increase the oxygen supply to sediments and hence the rates of organic matter decomposition and subsequent CaCO₃ dissolution. Similarly, seagrasses may facilitate CaCO₃ sediment dissolution by releasing oxygen through their rhizomes (Burdige & Zimmerman 2002; Burdige et al. 2008, 2010). Thus, the complex biogeochemistry of sediment pore waters can drive either net dissolution or precipitation of CaCO₃ mineral phases, depending upon the dominant governing process of a specific reef environment and the depth within the sediments.

Important Bioeroders and Rates of Bioerosion

Many reef organisms contribute to the physical breakdown of CaCO₃ by means of mechanical abrasion or active penetration of CaCO₃ substrates through the release of metabolic CO₂ or other acids that dissolve the CaCO₃. The biological destruction of reef material is collectively referred to as bioerosion (for reviews, see Hutchings 1986, Glynn 1997, Wisshak & Tapanila 2008). Fish and echinoderms (e.g., sea urchins) are typically the major grazers on coral reefs. In searching for food, they scrape and bite on the reef surface to ingest organic material, which consequently causes erosion and results in the production of sediments. Bite marks from parrotfish and/or other grazers are clearly visible in coral reef environments. Various molluscs (e.g., limpets, snails, and chitons) also contribute to bioerosion through grazing, but they are less important than fish and echinoderms. Many of these organisms utilize a mineral-enforced radula to scrape the surface. A number of microorganisms, including bacteria, fungi, and algae, colonize carbonate substrates

and actively penetrate these substrates by releasing acids (Radtke et al. 1997, Tribollet 2008). These boring microflora, which can be autotrophic or heterotrophic, are collectively referred to as euendoliths. Boring sponges are a significant source of bioerosion on coral reefs [see review by Schönberg (2008)]. The exact mechanism of destruction is not fully understood, but it probably involves a combination of mechanical and chemical erosion. Estimates suggest that 2%–75% of bored materials are dissolved and 25%–98% are disposed of as chips with a characteristic shape and morphology that can be identified in the sediments (Neumann 1966, Hutchings 1986, Schönberg 2008). Other bioeroders include foraminifera, crustaceans (e.g., barnacles, shrimps, and crabs), sipunculans (unsegmented marine worms), polychaetes (a class of annelid worms), and holothurians (e.g., sea cucumbers). A recent study investigating the role of sea cucumbers, which ingest carbonate sand and rubble when searching for food and as a consequence dissolve CaCO_3 in their digestive tracts, concluded that they were responsible for 50% to almost 100% of nighttime dissolution in two different environments investigated at One Tree Reef on the Great Barrier Reef (Schneider et al. 2011).

Numerous studies have attempted to quantify the magnitude of bioerosion caused by different organisms in order to evaluate their contributions to the CaCO_3 loss from reefs (for detailed reviews of the range of estimates, see Hutchings 1986, Glynn 1997, Wisshak & Tapanila 2008, and references therein). Based on existing estimates, bioerosion is a major component of the total erosion of reefs, but caution needs to be exercised in extrapolating the rates because they are likely not constant and vary between different reef habitats (Hutchings 1986). Bioerosion rates for any particular organism may vary significantly depending on the environment, the density and hardness of the substrate, and competition from other bioeroders (Trudgill 1976, Hutchings 1986). Furthermore, the loss of CaCO_3 owing to bioerosion could be due to physical breakdown and/or dissolution, and it is challenging to distinguish between the two processes and quantify the fate of the lost CaCO_3 .

Some of the highest bioerosion rates have been estimated for sponges (e.g., Neumann 1966, Rützler 1975, Hudson 1977, Hutchings 1986, Schönberg 2002), with rates ranging from 200 to as much as 23,000 $\text{g CaCO}_3 \text{ m}^{-2} \text{ sponge}^{-1} \text{ year}^{-1}$ (26 $\text{mmol m}^{-2} \text{ h}^{-1}$) (Neumann 1966, Glynn 1997). The extent of sponge bioerosion is also evident from the large abundance of sponge chips in sediments; Fütterer (1974) observed 30% of lagoonal sediments on Fanning Island to be made out of sponge chips, and Halley et al. (1977) observed 40% in the silt-size fraction within patch reefs in Belize.

High rates of bioerosion have also been attributed to fish grazing and echinoids, with estimates ranging from 70 to 22,300 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (0.08–25 $\text{mmol m}^{-2} \text{ h}^{-1}$) and from 30 to 9,100 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (0.03–10.4 $\text{mmol m}^{-2} \text{ h}^{-1}$), respectively (Glynn et al. 1972, Ogden 1977, Russo 1980, Kiene 1988, Bak 1990, Bellwood 1995, Glynn 1997). Similarly high rates have been estimated for an internal boring mollusc breaking down El Niño–damaged corals at a rate of 9,000 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (10 $\text{mmol m}^{-2} \text{ h}^{-1}$) (Scott et al. 1988). However, estimates for external boring molluscs range from 20 to 400 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (0.02–0.5 $\text{mmol m}^{-2} \text{ h}^{-1}$) (Glynn 1970, Donn & Boardman 1988).

Polychaetes are often the initial colonizers of newly available substrates, which may facilitate the recruitment of the sponges, sipunculans, and molluscs that are dominant in aged carbonate substrates (Hutchings 1986, 2008). Estimates of bioerosion rates owing to polychaetes alone range from 100 to 4,800 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (Davies & Hutchings 1983; Hutchings & Bamber 1985; Hutchings 1986, 2008; Peyrot-Clausade et al. 1992; Kiene & Hutchings 1994; Osorno et al. 2005). Colonization of boring microflora occurs in both live and dead carbonate substrates, although colonization appears to be greater in dead substrates (Radtke et al. 1997; Tribollet 2007, 2008). Rates of bioerosion due to microflora are in general lower than those due to sponges and grazers,



Alkalinity anomaly technique: a method to quantify NEC that assumes that the formation of 1 mol of CaCO_3 decreases seawater TA by 2 mol and DIC by 1 mol

with estimates ranging from less than 70 to 350 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ (0.08–0.4 $\text{mmol m}^{-2} \text{ h}^{-1}$) (Tudhope & Risk 1985; Chazottes et al. 1995, 2002; Tribollet 2008).

Rates of CaCO_3 Dissolution in Coral Reef Communities and Sediments

There is no doubt that bioerosion is an important process contributing to the breakdown and dissolution of CaCO_3 substrates on coral reefs (the latter implying the transition from a solid state of CaCO_3 to Ca^{2+} and CO_3^{2-} ions dissolved in seawater), but it is challenging to quantify the relative proportions of these processes and the precise contribution to the total coral reef gross dissolution. Gross dissolution is poorly understood, as most community-scale investigations of dissolution are based on the alkalinity anomaly technique and measure only the net of calcification and dissolution (Langdon et al. 2010, Andersson & Mackenzie 2012). Thus, most dissolution estimates reflect net dissolution at times or in environments where dissolution is believed to exceed calcification, such as at nighttime, when respiration produces CO_2 and may create undersaturation with respect to some CaCO_3 mineral phases (e.g., Conand et al. 1997; Yates & Halley 2003, 2006; Silverman et al. 2007a,b; Shamberger et al. 2011); in back reef environments and lagoons dominated by carbonate sand or mud; and/or in carbonate sediments.

Some investigators have made attempts to quantify gross dissolution using various approaches, but these attempts are few (e.g., Barnes & Devereux 1984, Silverman et al. 2007b, Andersson et al. 2009). If no calcification were taking place, net dissolution would obviously be equal to gross dissolution. Hence, observations of net dissolution represent minimum estimates of gross dissolution rates, which in general must be higher because biogenic calcification and/or inorganic precipitation of CaCO_3 may occur at all times, although calcification by organisms dependent on photosynthesis is significantly lower in dark than in light conditions (e.g., Gattuso et al. 1999). Furthermore, net dissolution estimates do not distinguish between dissolution from bioerosion and dissolution from metabolism, but rather represent the integrated effect of both processes.

Observations of net community dissolution under a range of environmental conditions and approaches, including both experimental and field settings, vary from 0 to 25 $\text{mmol m}^{-2} \text{ h}^{-1}$ (Table 1), although the majority of estimates are in the range of 0.1 to 4 $\text{mmol m}^{-2} \text{ h}^{-1}$. Expressed as grams per year to compare with the previously reported bioerosion rates, these estimates correspond to 0–21,900 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ and 90–350 $\text{g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$, respectively.

Net dissolution in natural coral reef environments based on alkalinity anomalies has been observed almost exclusively at nighttime, with some exceptions (Barnes & Devereux 1984; Kinsey 1985, 1988; Conand et al. 1997; Silverman et al. 2007a,b; Shamberger et al. 2011). Conand et al. (1997) observed marginal nighttime net dissolution on a reef flat and back reef environment at Réunion Island during the winter and similar dissolution on the reef flat during the summer. During the summer, the nighttime dissolution rates from the back reef were very high (25 $\text{mmol m}^{-2} \text{ h}^{-1}$) and significantly exceeded daytime calcification rates, resulting in a daily net dissolution of 3.8 $\text{mmol m}^{-2} \text{ h}^{-1}$. Similarly, preliminary data from the Bermuda coral reef platform during the winter indicate that seawater TA is at times replete relative to the source water of the Sargasso Sea, suggesting net dissolution on the platform during this time of the year (Bates et al. 2010). Similar observations have been made in Florida (C. Langdon, personal communication).

Silverman et al. (2007b) used two different approaches based on observed or calculated alkalinity repletion to estimate CaCO_3 dissolution on a coral reef in the Gulf of Aqaba, Red Sea. Dissolution ranged from 0.1 to 1.2 $\text{mmol m}^{-2} \text{ h}^{-1}$, with an average of 0.8 ± 0.4 and 0.5 ± 0.3 $\text{mmol m}^{-2} \text{ h}^{-1}$ for the two methods, respectively. These rates were at most equivalent to

Table 1 Carbonate dissolution rates reported from subtropical and tropical shallow carbonate environments and experimental settings (modified from Andersson et al. 2007)

Location	Environment	Dissolution rate (mmol m ⁻² h ⁻¹)	Reference(s)
Bahamas	Oolitic sand	0.0004	Burdige & Zimmerman 2002
Bahamas	Sparse to dense seagrass bed	0.008–0.04	Burdige & Zimmerman 2002
Bahamas	Seagrass bed in sandy sediments	0.01–1.1	Burdige et al. 2008
Bahamas	Seagrass bed in sandy sediments, LAI = 0–0.1 m ² m ⁻²	0.001–0.28	Burdige et al. 2010
Bahamas	Seagrass bed in sandy sediments, LAI = 0.24–0.96 m ² m ⁻²	0.14–0.93	Burdige et al. 2010
Bahamas	Seagrass bed in sandy sediments. LAI = 1.2–3.73 m ² m ⁻²	0.63–3.35	Burdige et al. 2010
Bermuda	Carbonate sediments	0.2–0.8	Andersson et al. 2007
Bermuda	Carbonate sediments	0.3	Balzer & Wefer 1981
Biosphere 2	High-Mg-calcite sediments	0.2	Langdon et al. 2000
Florida	Patch reef, 10% coral cover	0.5	Yates & Halley 2003
Florida	Patch reef, top	0.1	Yates & Halley 2003
Florida	Seagrass	0.4	Yates & Halley 2003
Florida	Sand bottom	0.3	Yates & Halley 2003
Florida	Seagrass, red algae	0.4	Walter & Burton 1990
Florida	Mangrove, red algae	0.8	Walter & Burton 1990
Florida	Carbonate sediments	0.25–0.29	Rude & Aller 1991
Great Barrier Reef	Reef flat	4 (daily gross)	Barnes & Devereux 1984
Hawaii	Patch reef, 22% coral cover	0.3–3.0	Yates & Halley 2006
Hawaii	Patch reef, 10% coral cover	0.1–0.5	Yates & Halley 2006
Hawaii	Coral rubble	0.2–2.0	Yates & Halley 2006
Hawaii	Sand bottom	0.05–0.6	Yates & Halley 2006
Kaneohe Bay, Hawaii	Mesocosm (<i>n</i> = 3) ^a	0.04 (SD = 1.1) (future conditions daily average) 2.2 (SD = 1.3) (ambient conditions maximum at night) 3.6 (SD = 1.9) (future conditions maximum at night)	Andersson et al. 2009
Kaneohe Bay, Hawaii	Lagoon exposed to extensive organic matter loading from sewage	7.4	Kinsey 1985
Monaco mesocosm	Sand community	0.8	Leclercq et al. 2002
Moorea, French Polynesia	Sandy bottom reef flat and lagoon	0.8	Boucher et al. 1998
Red Sea	Reef, 20%–40% coral cover	0.5–0.8 (average) 0.1–1.2 (range)	Silverman et al. 2007a,b
Réunion Island	Back reef zone	1.7 (annual average) 3.8 (daily average, summer) 25 (maximum at night, summer)	Conand et al. 1997

Abbreviation: LAI, leaf area index.

^aDissolution rates represent the average for three mesocosms.

approximately 30% of the annual average gross community calcification rate. No seasonal trend was apparent in the dissolution rates at this location. Barnes & Devereux (1984) observed net dissolution at nighttime along a transect on the reef flat of Rib Reef on the Great Barrier Reef. The nighttime rates of net dissolution were approximately $2 \text{ mmol m}^{-2} \text{ h}^{-1}$. Based on relationships between light intensity and net calcification rates, the authors calculated that the gross dissolution on a daily basis was equal to $4 \pm 3.4 \text{ mmol m}^{-2} \text{ h}^{-1}$. Yates & Halley (2003, 2006) used an enclosed, transparent incubation chamber called SHARQ (Submersible Habitat for Analyzing Reef Quality) to estimate reef community metabolism for different benthic substrates in Florida and Hawaii. Net dissolution was observed primarily at nighttime, although on occasion net dissolution was also observed during daytime on sand bottom substrate. Nonetheless, the highest rates of hourly net dissolution were observed in coral rubble and on a patch reef with 22% coral cover (Yates & Halley 2003, 2006). Similar to observations from the natural environment, experiments conducted in mesocosms and the Biosphere 2 facility have shown evidence of net dissolution primarily at nighttime (e.g., Langdon et al. 2000, 2003; Leclercq et al. 2000, 2002; Andersson et al. 2009).

It has been widely recognized that CaCO_3 dissolution is taking place in the sediments of tropical shallow water environments (Berner 1966; Balzer & Wefer 1981; Morse et al. 1985, 1987; Moulin et al. 1985; Walter & Burton 1990; Rude & Aller 1991; Walter et al. 1993; Ku et al. 1999; Burdige & Zimmerman 2002; Andersson et al. 2007; Hu & Burdige 2007; Burdige et al. 2008, 2010), but the rates of dissolution and resulting fluxes are variable. Part of this is due to the fact that the magnitude of dissolution is controlled by a number of parameters that are highly variable in shallow water sediments, such as organic matter content, mineral composition, grain size distribution, permeability, and porosity.

Burdige and colleagues (Burdige & Zimmerman 2002; Hu & Burdige 2007; Burdige et al. 2008, 2010) have devoted significant effort to investigating rates of dissolution in permeable sediments on the Bahama Banks. Specifically, they have evaluated the influence of seagrasses on CaCO_3 sediment dissolution, which may increase dissolution rates owing to provisioning of organic material, respiration, pumping of oxygen via rhizomes, and reduction of the physical flow of seawater, which is hypothesized to retain organic material in the area. However, reduced flow may decrease advection and flushing of the sediments, which may reduce the resulting flux of solutes. In general, dissolution rates appear to increase linearly with the seagrass density, a trend attributed mainly to oxygen pumping by the seagrasses (Burdige & Zimmerman 2002, Burdige et al. 2008).

Walter & Burton (1990) estimated the dissolution rates for substrates of red algae (18 mol% MgCO_3), echinoids (12 mol% MgCO_3), and corals (aragonite) submerged in natural carbonate sediments at depths ranging from 0 to 30 cm for 1 year. Based on weight loss, the calculated dissolution rates for the red algae ranged from $0.4 \text{ mmol m}^{-2} \text{ h}^{-1}$ in an area of substantial seagrass cover to $0.8 \text{ mmol m}^{-2} \text{ h}^{-1}$ in an area dominated by mangroves. Neither the echinoid nor the coral substrate showed evidence of dissolution rates as high as those of the red algae, and the mass loss of these substrates ranged from 2% to 9% of the dissolved mass of the algae. The observed differences in dissolution rates between substrates were consistent with their mineral composition and reactive surface area (Walter & Burton 1990, Walter et al. 1993, Ku et al. 1999).

Other investigators have calculated sediment dissolution rates by using observed gradients and laws of diffusion or advective transport models, or by using flux chambers (e.g., Balzer & Wefer 1981, Andersson et al. 2007). The estimated rates of community and sediment CaCO_3 dissolution are in general significantly lower than the rates of CaCO_3 loss attributed to various bioeroders, but it is inappropriate to compare these rates directly because the latter do not explicitly account for the proportion of CaCO_3 that is dissolved in most of the cases.



THE EFFECT OF OCEAN ACIDIFICATION AND CLIMATE CHANGE ON THE BREAKDOWN, EXPORT, AND DISSOLUTION OF CaCO_3

As a result of global warming and increasing heat content in the oceans, it is possible that the frequency and intensity of storms and hurricanes could increase (Intergov. Panel Clim. Change 2007). Similarly, coral bleaching events may also increase owing to warmer sea surface temperatures (e.g., Glynn 1991, Hoegh-Guldberg et al. 2007, Baker et al. 2008, Pandolfi et al. 2011). These changes would undoubtedly contribute to increasing CaCO_3 physical breakdown and export from coral reef environments.

Chemical dissolution could also accelerate with increasing OA. Although subtropical and tropical surface seawater is currently supersaturated with respect to the most commonly occurring CaCO_3 mineral phases, seawater could become undersaturated with respect to the average Mg calcite composition of coral reef sediments (13–15 mol% MgCO_3) (Chave 1967, Morse et al. 2006, Andersson et al. 2008). However, large uncertainty is associated with the solubility and reactivity of biogenic Mg calcite mineral phases in the natural environment owing to conflicting data from solubility experiments, and the precise chemical threshold when a particular Mg calcite phase becomes undersaturated is not well constrained (Morse et al. 2006, Andersson et al. 2008).

Furthermore, it might be expected that metabolic dissolution and bioerosion will increase with OA if the acid generation from these processes remains unchanged (**Figure 2**). However, the projected change in average surface seawater pH within the next century or so (~ 8.1 to ~ 7.8 – 7.9 ; e.g., Caldeira & Wickett 2003, Orr 2011) is small compared with the dynamic range currently

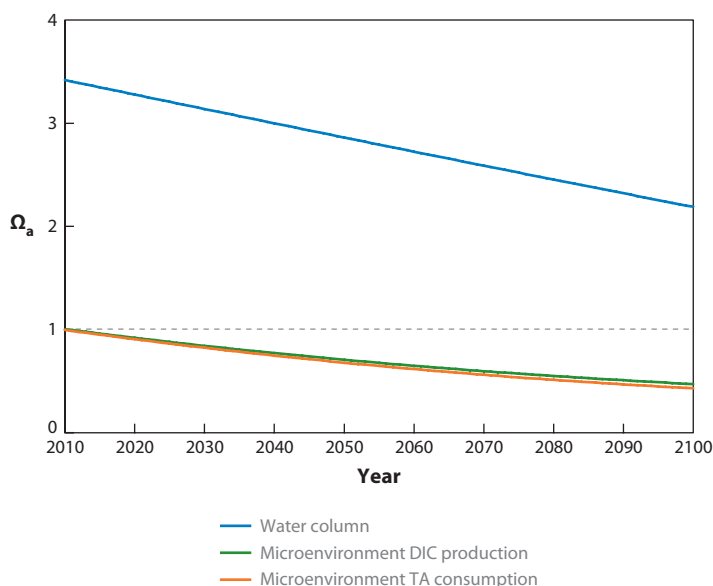


Figure 2

Hypothetical decrease in average coral reef seawater aragonite saturation state (Ω_a) (blue line) during the present century, assuming constant temperature ($T = 25^\circ\text{C}$), salinity ($S = 35$), and total alkalinity ($\text{TA} = 2,350 \mu\text{mol kg}^{-1}$) and an initial dissolved inorganic carbon (DIC) value of $2,050 \mu\text{mol kg}^{-1}$. The green and orange lines represent the resulting Ω_a within hypothetical microenvironments due to the generation of a fixed amount of CO_2 (DIC production) and acid (TA consumption) independent of time resulting from the respiration/decomposition of organic matter and an acid-producing bioeroder, respectively. The potential dissolution or precipitation of CaCO_3 was not considered in the calculation.

exhibited in sediment pore waters owing to the remineralization of organic matter, which can drive pore water pH to ranges of 7.0–7.4 (e.g., Morse et al. 1985, Walter & Burton 1990). Still, there is a limited understanding of how the carbonic acid chemistry and the carbonate saturation state in pore waters and microenvironments will be affected by water column OA. Although the pore water chemistry may be controlled primarily by the amount and rate of microbial decomposition of organic material (e.g., Leclercq et al. 2002, Andersson et al. 2003), the initial solution composition of this process starts with the overlying surface seawater. Nevertheless, this hypothesis still needs to be tested and verified. Metabolic dissolution and bioerosion could also increase should marine calcifiers deposit weaker and less dense CaCO_3 shells and skeletons (Buddemeier et al. 2004), making it easier to break down CaCO_3 substrates both physically and chemically (Hutchings 1986). As metabolic rates are also expected to accelerate with rising sea surface temperatures, it can be anticipated that both bioerosion and microbial remineralization would correspondingly increase.

Few studies have investigated the effects of OA on bioerosion and CaCO_3 dissolution, and we know little about the quantitative effects. Andersson et al. (2009) observed a significant increase in nighttime dissolution for replicated ($n = 3$) subtropical coral reef communities incubated in continuous-flow mesocosms exposed to a daily average $p\text{CO}_2$ of $\sim 1,147 \mu\text{atm}$ and a Ω_a of 1.4, compared with ambient conditions of $\sim 568 \text{ matm}$ and a Ω_a of 2.8. On a daily basis, communities exposed to elevated CO_2 lost on average $0.1 \text{ mmol m}^{-2} \text{ h}^{-1}$, whereas communities exposed to ambient conditions gained $3.3 \text{ mmol m}^{-2} \text{ h}^{-1}$. Andersson et al. (2009) attributed the observed change to a 24% decrease in calcification and a 138% increase in dissolution.

Tribollet et al. (2009) experimentally demonstrated increased bioerosion rates under high- CO_2 conditions. They exposed blocks of *Porites lobata* colonized with natural euendolithic and epilithic communities to different seawater $p\text{CO}_2$ conditions ($436 \pm 90 \mu\text{atm}$ and $758 \pm 111 \mu\text{atm}$) for 3 months. The bioerosion rate under the high- CO_2 conditions was significantly higher, and blocks lost $460 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ ($0.53 \text{ mmol m}^{-2} \text{ h}^{-1}$) compared with $310 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ ($0.35 \text{ mmol m}^{-2} \text{ h}^{-1}$) under ambient conditions.

These experimental findings appear to be consistent with field studies that have examined contemporary reef environments exposed to elevated CO_2 . Although not perfectly analogous to future OA conditions, high rates of bioerosion, low cementation, and poorly developed reefs were reported from the eastern tropical Pacific, which naturally experiences high CO_2 , low pH, and low Ω but also high nutrient concentrations owing to upwelling (e.g., Manzello et al. 2008, Manzello 2010). Similarly, Fabricius et al. (2011) investigated a coral reef in Papua New Guinea exposed to low pH and Ω as a result of a volcanic CO_2 vent, and although CaCO_3 dissolution was not explicitly investigated, reef accretion and development were not observed below an average seawater pH of 7.7.

CORAL REEF NET ECOSYSTEM CALCIFICATION

Because NEC represents the total sum of CaCO_3 production and dissolution processes, it is necessary to consider the effect of OA on both of these processes to accurately predict the effect of OA on NEC. The majority of studies investigating the effect of OA on coral and algal calcification have shown a consistent decline in calcification rates (for reviews, see Andersson et al. 2011, Erez et al. 2011, Pandolfi et al. 2011). However, a number of recent studies have indicated that some marine organisms' ability to calcify may not be sensitive to OA, although a satisfactory explanation for this has not been put forward (e.g., Ries et al. 2009). Furthermore, a recent study proposed that certain corals are able to upregulate calcification and will not be significantly negatively affected by OA (McCulloch et al. 2012). Nevertheless, from a coral reef ecosystem perspective, this may

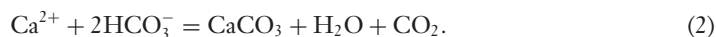


provide little relief if the CaCO_3 loss processes described above significantly increase in response to OA to the extent that NEC becomes negative and reef erosion exceeds accretion.

Past and Present Estimates of Net CaCO_3 Accretion and Net Ecosystem Calcification

Up until the mid-1970s, the surplus CaCO_3 production was estimated primarily by geological means, using vertical accretion rates, radio isotopic measurements (see Mayor 1918; Odum & Odum 1955; Chave et al. 1972 and references therein), or scaling up of potential calcification rates from community census (Smith 1973). Using the molecular weight of CaCO_3 ($100.09 \text{ g mol}^{-1}$), an assumed density of 2.89 g cm^{-3} , and an assumed porosity of 50% (Chave et al. 1972), these vertical rates (in millimeters per year) can be converted to net community CaCO_3 accretion rates (in millimoles per square meter per unit time). Using this approach, we find that these early estimates of net accretion yield rates ranging from $14 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ (Easton & Olson 1976) to more than $600 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ (Odum & Odum 1955) (Table 2). This range corresponds to $500\text{--}22,000 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$. It is important to consider, however, that vertical accretion represents rates averaged across thousands of years and can reflect changes in sea level rise and local tectonic adjustment as well as CaCO_3 import and export processes, which can all significantly influence the observed vertical accretion rates (Kinsey 1982).

Beginning in the 1970s, many investigations started using techniques first employed by Odum & Odum (1955) whereby coral “community metabolism” is measured from observed changes in water column chemistry. This approach is based upon the premise that although a community cannot strictly be described as exhibiting a metabolism per se, it is possible and valuable to describe the integrated performance of the ecosystem in terms of the rates at which metabolically relevant chemical species (e.g., DIC, TA, dissolved oxygen, and nutrients) are modified within the overlying water column (e.g., Smith 1973; Smith & Jokiel 1975; Kinsey 1979a,b, 1985; Atkinson & Grigg 1984; Barnes & Devereux 1984; Suzuki et al. 1995; Gattuso et al. 1996; Ohde & van Woesik 1999; Silverman et al. 2007a,b; Shamberger et al. 2011). In the case of calcification, changes in seawater TA are commonly monitored, as the process consumes 2 mol of TA for each 1 mol of CaCO_3 , produced according to the equation



Thus, the time rate of change in TA can be applied to derive NEC rates (e.g., Smith 1973, Smith & Key 1975, Smith & Kinsey 1978).

There are at least two methods that have been employed to directly measure NEC: enclosure and flow respirometry. Enclosure methods involve a confined system either naturally (e.g., a “slack water” method such as the one used in Kinsey 1979b) or experimentally (as is the case with incubation chambers or mesocosms; e.g., Atkinson & Grigg 1984; Yates & Halley 2003, 2006; Andersson et al. 2009). The flow respirometry method commonly uses an Eulerian approach with paired upstream and downstream measurements of TA multiplied by volume transport per unit length of the reef community divided by the transit length according to (Smith 1973, Langdon et al. 2010)

$$\text{NEC} = \frac{\Delta T \, A b \rho}{2 \Delta t}, \quad (3)$$

where ΔT is the difference between upstream and downstream TA concentrations (in millimoles per kilogram), b is the average water depth along which the water transits (in meters), ρ is the density of seawater (in kilograms per cubic meter), and Δt is the transit time of the water across the reef. A Lagrangian approach can also be adopted whereby ΔT is tracked within a parcel of



Table 2 Summary of estimates of net ecosystem calcification (NEC) or accretion rates from different coral reef environments

Location	Method/environment/other remark	NEC or vertical accretion	Reported units	NEC or net accretion (mmol m ⁻² day ⁻¹)	Reference
American Samoa	Geological/reef flat	1,606	g m ⁻² year ⁻¹	44	Mayor 1918
Bermuda	Geological/boiler reefs	1,400	g m ⁻² year ⁻¹	38	Schroeder & Ginsburg 1971 ^a
Bermuda	Flow respirometry/annual range	-2.2–10.4	g m ⁻² day ⁻¹	-22–104	Bates et al. 2010
Bikini Atoll	Geological/general	1,400	g m ⁻² year ⁻¹	38	Emery et al. 1954 ^a
Bikini Atoll	Geological/lagoon	5,400	g m ⁻² year ⁻¹	148	Emery et al. 1954 ^a
Biosphere 2 (modern conditions)	Enclosure/mixed community			75	Langdon et al. 2000
Biosphere 2 (experimental manipulations)	Enclosure/mixed community/ $\Omega_a = 1.6, 3.1, 5.2$			5, 40, 115	Langdon et al. 2000
Biosphere 2 (experimental manipulations)	Enclosure/mixed community/ $\Omega_a = 2.3, 2.8$			6, 41	Langdon et al. 2003
Canton Atoll	Flow respirometry/reef with deep lagoon			14	Smith & Jokiel 1978 ^b
Christmas Island	Flow respirometry/reef with flat and shallow lagoon			2.5	Smith et al. 1984 ^b
Coconut Island, Hawaii	Enclosure/ <i>Porites compressa</i> and <i>Montipora verrucosa</i> /ambient CO ₂	15.4–16	mmol m ⁻² h ⁻¹	185–192	Langdon & Atkinson 2005
Coconut Island, Hawaii	Enclosure/ <i>Porites compressa</i> and <i>Montipora verrucosa</i> /1.3–1.7 times ambient CO ₂	9–12	mmol m ⁻² h ⁻¹	108–144	Langdon & Atkinson 2005
Coconut Island, Hawaii	Enclosure/mixed community/ambient CO ₂	3.3	mmol m ⁻² h ⁻¹	79	Andersson et al. 2009
Coconut Island, Hawaii	Enclosure/mixed community/2 times ambient CO ₂	-0.04	mmol m ⁻² h ⁻¹	-1	Andersson et al. 2009
Eilat, Israel	Flow respirometry/fringing reef	16.3	g m ⁻² day ⁻¹	163	Barnes & Lazar 1993
Enewetak Atoll	Geological/windward reef community	0.016	m year ⁻¹	633	Odum & Odum 1955
Fanning Atoll	Flow respirometry/reef with deep lagoon			27	Smith & Pesret 1974 ^b
Fiji	Geological/channel across reef	2,200	g m ⁻² year ⁻¹	60	Gardiner 1903 ^a
Florida	Geological/Key Largo reef	8,100	g m ⁻² year ⁻¹	222	Hoffmeister & Multer 1964
French Frigate Shoals	Flow respirometry/reef flat/range winter–summer			77–279	Atkinson & Grigg 1984
French Frigate Shoals	Flow respirometry/lagoon/winter			38	Atkinson & Grigg 1984
Gulf of Aqaba, Red Sea	Flow respirometry/fringing reef/range winter–summer			30–60	Silverman et al. 2007 ^b
Hawaii	Geological/reef community	1,400	g m ⁻² year ⁻¹	38	B.L. Oostdam, unpublished data ^a

Hawaii	Geological/reef flat	7,400	$\text{g m}^{-2} \text{ year}^{-1}$	203	Easton 1969 ^a
Hawaii (5,800 to 3,500 years before present)	Geological	0.0030	m year^{-1}	132	Easton & Olson 1976
Hawaii (past 3,500 years)	Geological	0.0003	m year^{-1}	14	Easton & Olson 1976
Jamaica	Geological/reef slope	1,600	$\text{g m}^{-2} \text{ year}^{-1}$	44	Goreau & Land 1974 ^a
Jamaica	Flow respirometry/reef crest to back reef			120	Kinsey 1982
Kaneohe Bay, Hawaii	Flow respirometry/fringing reef edge and patch reef			246–301	Kinsey 1979 ^{a,c}
Kaneohe Bay, Hawaii	Flow respirometry/barrier reef/range summer–winter			174–331	Shamberger et al. 2011
Lizard Island, Great Barrier Reef	Flow respirometry/outer reef flat/October–December			100	Kinsey 1977
Lizard Island, Great Barrier Reef	Flow respirometry/patch reef and lagoon reef			109–137	Kinsey 1979 ^{a,c}
Lizard Island, Great Barrier Reef	Flow respirometry/complete reef			49	Kinsey & Davies 1979 ^c
Majuro Atoll	Flow respirometry/reef with deep lagoon			141	Suzuki et al. 1997 ^b
Moorea, French Polynesia	Flow respirometry/reef flat	22	$\text{g m}^{-2} \text{ day}^{-1}$	220	Gattuso et al. 1993
Moorea, French Polynesia	Flow respirometry/back reef	24.3	$\text{g m}^{-2} \text{ day}^{-1}$	243	Gattuso et al. 1996
Ningaloo Reef, Western Australia	Flow respirometry/reef flat			200	Falter et al. 2012
Okinawa, Japan	Enclosure/reef flat daytime	9	$\text{mmol m}^{-2} \text{ h}^{-1}$	108	Ohde & van Woesik 1999
One Tree Island, Great Barrier Reef	Flow respirometry/reef slope to lagoon			40	Kinsey 1977
One Tree Island, Great Barrier Reef	Flow respirometry/outer reef flat/seasonal range			110–145	Kinsey 1977
Rib Reef, Great Barrier Reef	Flow respirometry/reef flat	9.4	$\text{g m}^{-2} \text{ day}^{-1}$	94	Barnes & Devereux 1984
Shiraho Reef, Ishigaki Island, Japan	Flow respirometry/reef flat with shallow lagoon			100	Kayanne et al. 1995 ^b
Shiraho Reef, Ishigaki Island, Japan	Enclosure/mixed coral community			1.2	Nakamura & Nakamori 2008

^aAs reported in Chave et al. 1972.^bAs reported in Suzuki & Kawahata 2003.^cAs reported in Kinsey 1985.

water over time using a drifter or drogue. In all cases, it is important to consider that the resulting units of NEC adopt a planar surface area (in square meters), which has important implications with regard to interpreting the magnitude of NEC that has been reported as a function of Ω_a (Figure 1). Apparent correlations between NEC and Ω_a can be described by the general rate equation, which has been previously applied to describe inorganic carbonate mineral kinetics (Morse & Arvidson 2002). However, in the application of the general rate equation, it is imperative that the total reactive surface area be rigorously evaluated so that comparisons between experimental results can be made. No such standardized normalization methodology has been developed for the application of the general rate equation in describing community-scale kinetics.

Estimates of NEC based upon community metabolism from different reef environments yield a broad range of rates, from $-22 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ (Bates et al. 2010) to $331 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ (Shamberger et al. 2011), equivalent to -800 to $12,100 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$. Even experimental enclosure-based estimates at ambient conditions yield divergent rates, ranging from $1 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ (Nakamura & Nakamori 2008) to about $200 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ (Langdon & Atkinson 2005) (Table 2). However, these data cannot be directly compared on a simple basis, as the reported rates represent different reef environments, experimental settings, seawater physical-chemical conditions, and temporal and spatial scales. For example, some estimates represent diurnal averages whereas others report annual averages, and some rates are representative of a whole reef system whereas others represent a specific area or habitat of a reef.

Based on observations from eight different reefs, mainly in the Pacific, Smith & Kinsey (1976) suggested that NEC rates are highly uniform for these systems if one considers a simple bimodal reef zonation: seaward reef flats and protected lagoonal environments characterized by annual average NEC rates of 109 ± 8 and $22 \pm 11 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ ($4,000$ and $800 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$), respectively. Kinsey (1979a, 1982, 1985) elaborated on this idea further using data from the literature and proposed three absolute modes of coral reef calcification based on 100% hard coral/algal substratum (upper rate limit), 100% algal pavement, and 100% sand and rubble (lower rate limit), with approximate net calcification rates of 274 , 109 , and $14 \text{ mmol CaCO}_3 \text{ m}^{-2} \text{ day}^{-1}$ ($10,000$, $4,000$, and $500 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$), respectively. Smith (1978) suggested that, on average for the world's coral reefs, 1%–2% of the area on a reef calcifies at the higher rate, 4%–8% calcifies at the intermediate rate, and 90%–95% calcifies at the lower rate associated with these different modes. Nonetheless, it is important to recognize that these generalized areas and rates are derived as averages for the majority of the world's reefs and do not necessarily apply to any one reef.

Based on the reported rates of net accretion and NEC, it is apparent that considerable care must be employed when comparing these rates across different environments and across timescales ranging from hours to thousands of years. Long-term net accretion rates represent the integration of all constructive and destructive processes, including not only calcification and dissolution but also mass wasting, import, and export processes not apparent in short-term estimates based on changes in water column chemistry. Another important consideration when obtaining field estimates of NEC is that it is quite variable both temporally and spatially. Furthermore, as discussed above, it has been well demonstrated that many factors beyond carbonate chemistry impart an important control of NEC. Thus, comparisons between different reefs and the scaling of short-term (hourly) NEC estimates to annual or even daily rates require caution.

Net Ecosystem Calcification and Ocean Acidification

Identifying metrics of change that can be specifically attributed to the effects of OA within coral reef ecosystems is an emerging requirement as we look toward monitoring the impacts over the



next century. Although it is apparent that there will be a diversity of species-specific responses to OA, with some exhibiting more tolerance and others exhibiting less, the prevailing expectation remains that at the community scale there will be a tendency toward reduction in overall CaCO_3 production. Together with the likely increased rates of bioerosion and dissolution, it seems probable that NEC will decline over the coming decades.

A number of studies have investigated how NEC varies as a function of both controlled and naturally changing seawater Ω_a and have attempted to define geochemical thresholds at which dissolution exceeds calcification at experimental, local, and global scales (Langdon et al. 2000, 2003; Leclercq et al. 2000, 2002; Yates & Halley 2003, 2006; Silverman et al. 2007a,b, 2009; Andersson et al. 2009; Shamberger et al. 2011). The results have varied significantly depending on the study and the environment. For example, Silverman et al. (2009) proposed that all coral reefs would cease net positive accretion and undergo net dissolution at an atmospheric CO_2 concentration of 560 ppm, taking into account the effects of both warming and OA. Yates & Halley (2006) reported a range of seawater $p\text{CO}_2$ thresholds (467–1,003 μatm) at which $\text{NEC} = 0$ for different coral reef habitats. Andersson et al. (2009) observed a transition from net accumulation to net loss of CaCO_3 at a seawater $p\text{CO}_2$ of 1,147 μatm in replicated mesocosm experiments. Regardless of the precise seawater conditions when $\text{NEC} = 0$, essentially all studies have shown decreasing NEC as a function of decreasing seawater Ω_a . Based on the derived relationships between NEC and Ω_a (and assuming these relationships are accurate), a reduction in average Ω_a by 1 unit could result in a decline in NEC of 15%–130% (see summary in Andersson et al. 2011). However, reducing our predictive uncertainty and/or monitoring NEC over time to interpret OA impacts will prove challenging if we are unable to reconcile the apparent differences observed in the relationships between NEC and Ω_a (**Figure 1**).

As a first step, it is critical that we understand what is controlling the magnitude and dependence (i.e., slope) of the observed correlation between NEC and Ω_a . It should be recognized that the relationships established over diel or seasonal cycles do not necessarily reflect a functional relationship between these two parameters. NEC is directly or indirectly affected by a number of parameters in addition to seawater CO_2 chemistry, including light, temperature, nutrition, and hydrography (e.g., Kleypas et al. 1999b, 2001). Furthermore, seawater Ω_a is a function of the concentration of DIC relative to that of TA as well as temperature and salinity.

Changes in DIC and TA reflect whole-reef-community metabolism, including both NEC and NEP. The net effect of these processes can be evaluated using a graphical approach based on a property-property plot of DIC and TA where the reaction path can take on variable slopes depending on the ratio of organic to inorganic carbon production and consumption (Deffeyes 1965, Suzuki & Kawahata 2003). Furthermore, different net reaction paths (or slopes in the property-property plot) can yield different changes in seawater Ω_a (**Figure 3**). For example, if DIC and TA change at a ratio of $\sim 1.05:1$ (at DIC and TA concentrations typically observed on coral reefs at the present time, and assuming a constant temperature of 25°C and a salinity of 35), then seawater Ω_a remains essentially constant regardless of the rate at which these changes occur. In contrast, if calcification is the only process occurring within a system—i.e., DIC and TA decrease at a ratio of $1:2$ —then the result is a decrease in seawater Ω_a ; if primary production exceeds calcification, then a change in DIC and TA at a ratio greater than $1.05:1$ results in an increase in seawater Ω_a (**Figure 3**). Hence, in evaluating how NEC changes as a function of Ω_a , one needs to consider the net community metabolic effect of changing DIC and TA because this will affect not only the reaction path as diagrammed in the property-property plot but also the slope of the relationship between NEC and Ω_a . Furthermore, the rate of NEC also affects this relationship.

Figure 4 illustrates the resulting changes in Ω_a following three hypothetical reaction paths under three scenarios at different NEC rates (constant, increasing, and decreasing). From these



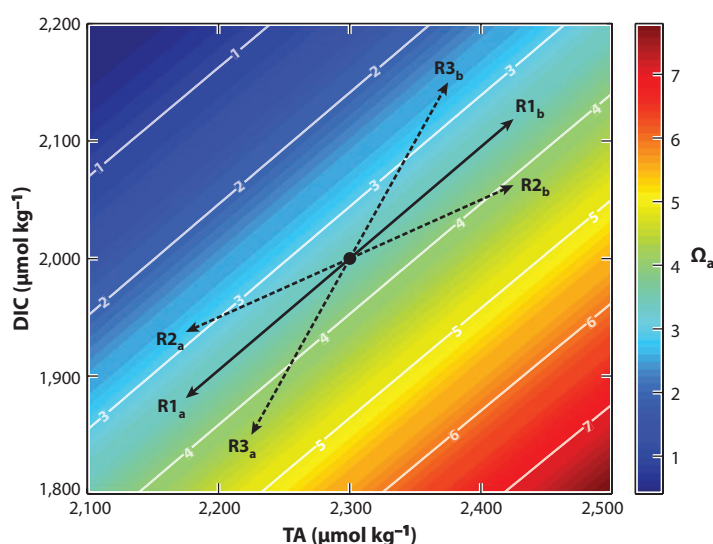


Figure 3

Contour plot of seawater aragonite saturation state (Ω_a) as a function of total dissolved inorganic carbon (DIC) and total alkalinity (TA) at a temperature of 25°C and a salinity of 35. The reaction pathways (R1–R3) show the resulting Ω_a if net reef metabolism (net ecosystem calcification and net ecosystem production) changes DIC and TA following $\Delta\text{DIC}/\Delta\text{TA}$ of 1.05 (R1), 0.5 (R2), and 2 (R3) from a starting condition represented by the solid black circle. A subscript of *a* denotes net reactions consuming DIC and TA; a subscript of *b* denotes net reactions producing DIC and TA.

hypothetical scenarios, it is evident that the observed relationship between NEC and Ω_a is controlled by both the relative change in DIC:TA and the rate of the reaction. The complexity of the problem arises from the fact that biogeochemical processes are strongly coupled and controlled by a number of factors that covary. For example, photosynthesis is strongly coupled to light. As photosynthesis increases in (for example) corals or algae in response to light, energy is generated that may facilitate the calcification process. In addition, depending on the resulting change in DIC:TA owing to these two processes, the resulting change in seawater CO_2 chemistry may promote calcification if Ω_a increases and pH decreases (i.e., $\text{DIC:TA} > 1.05$). Similarly, the extent of CaCO_3 dissolution occurring mainly in microenvironments and sediment pore waters is strongly linked to the extent and rates of organic matter decomposition, which becomes dominant at nighttime in the absence of photosynthesis. Hence, establishing quantitative functional relationships between NEC and Ω_a requires performing experiments at different seawater CO_2 conditions while keeping other parameters, such as light, temperature, and nutrients, the same across treatments.

Figure 5 shows the DIC:TA relationships and NEC as a function of Ω_a resulting from a diurnal mesocosm experiment with identical coral communities (40 colonies of *Montipora capitata*) exposed to ambient or approximately double ambient $p\text{CO}_2$ conditions (Andersson et al. 2009). The $p\text{CO}_2$ manipulation was conducted by acid addition, and hence lower TA was observed in the treatment conditions. Notably, the DIC:TA dependence remained more or less unchanged between the treatment and control conditions, which probably reflects the identical communities and the fact that light and temperature were essentially the same between the mesocosms (**Figure 5a**). Although the DIC:TA relationship remained similar, the range of change in DIC and TA under the treatment conditions was less than that under the control conditions. Evaluation of NEC as a function of Ω_a shows that the intercept where $\text{NEC} = 0$ under the treatment

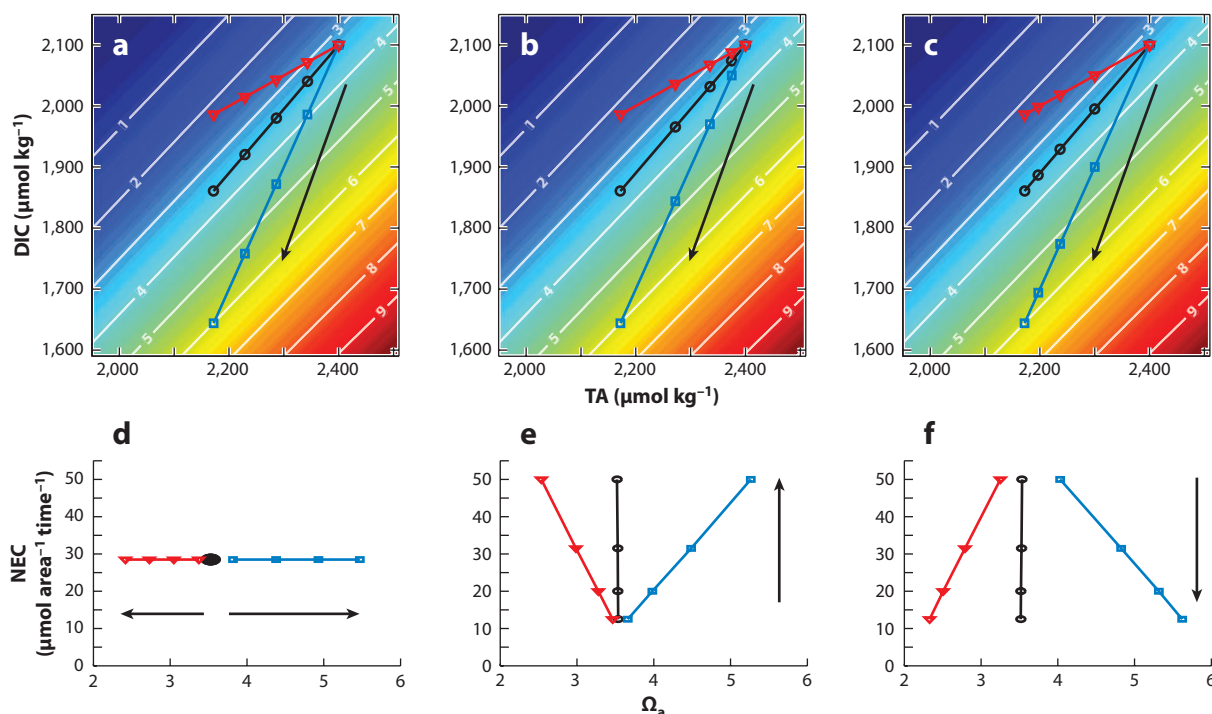


Figure 4

Three hypothetical reaction paths [starting at dissolved inorganic carbon (DIC) = 2,100 $\mu\text{mol kg}^{-1}$ and total alkalinity (TA) = 2,400 $\mu\text{mol kg}^{-1}$] owing to net reef metabolism ($\Delta\text{DIC}/\Delta\text{TA}$; black = 1.05, red = 0.5, blue = 2) at constant temperature (25°C) and salinity (35) superimposed on the resulting seawater aragonite saturation state (Ω_a ; contours). Black arrows show the direction of the reaction. For each reaction path, the rate of change in DIC and TA was altered without changing $\Delta\text{DIC}/\Delta\text{TA}$ from a constant rate (panels *a* and *d*), increasing rate (panels *b* and *e*), or decreasing rate (panels *c* and *f*), respectively. Panels *d–f* show the resulting relationships between net ecosystem calcification (NEC) and Ω_a for each reaction scenario. The figure demonstrates that plots of NEC as a function of Ω do not reveal a functional relationship between these two parameters; rather, the resulting change in seawater Ω owing to the combined effect of the rate of change of NEC and net ecosystem production (NEP) and the specific reaction path—i.e., the slope of the line (NEC versus Ω)—may change owing to the rate of change in NEC or as a function of the reaction path.

conditions occurred at seawater Ω_a significantly lower (1.46) than that under the control conditions (2.08). Furthermore, although the data are scattered, the slope of the relationship under the treatment conditions is less than that under the control conditions (**Figure 5b**).

These results highlight the need for caution in interpreting the relationships of NEC as a function of Ω_a derived from natural diel and seasonal cycles and in extrapolating these relationships to different reef systems over time without consideration of the net reef metabolism, including both NEC and NEP. Although these types of studies are important and critical to understanding the function and biogeochemistry of coral reefs, the relationship between NEC and Ω_a does not necessarily represent a functional relationship; it more likely represents the rate of NEC as a function of the net effect of the total reef metabolism on the seawater Ω_a . NEC rates might prove more interpretable when other concomitant processes such as NEP are considered in tandem. Monitoring of NEC- Ω_a relationships combined with property-property plots of DIC and TA for a given reef system reveals the system-level performance of the carbon cycle of that system (Suzuki & Kawahata 2003). This approach may provide a powerful tool to monitor the performance and function of coral reefs, may help to resolve some of the disparity between different studies, and

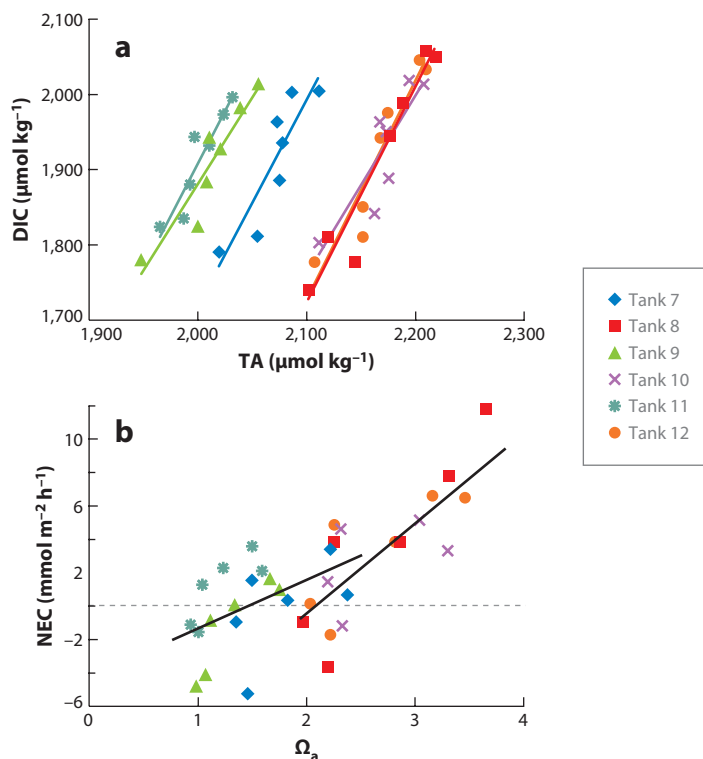


Figure 5

(a) Dissolved inorganic carbon (DIC) and total alkalinity (TA) measured over a 24-h period in continuous-flow mesocosms containing subtropical coral reef communities dominated by the coral *Montipora capitata* exposed to ambient (tanks 8, 10, and 12) and approximately double ambient (tanks 7, 9, and 11) seawater $p\text{CO}_2$. The average slopes of the best-fit lines equal 2.7 and 2.6 for the control and treatment conditions, respectively. (b) Calculated net ecosystem calcification (NEC) as a function of aragonite saturation state (Ω_a) for the mesocosms. Data from Andersson et al. (2009).

potentially offers a valuable method for tracking the long-term effects of OA and climate change on coral reefs.

SUMMARY POINTS

1. The construction of complex carbonate structures on coral reefs is essential in providing habitats for a large number of species and maintaining the extraordinary biodiversity associated with these ecosystems.
2. The persistence of coral reefs is dependent on the production and deposition of CaCO_3 exceeding the loss of CaCO_3 via breakdown, export, and dissolution processes.
3. Little attention has been paid to the effect of OA on bioerosion and CaCO_3 dissolution on coral reefs even though these processes are critical for evaluating their net growth and persistence. Based on theory, experiments, and field observations, the probability is high that these processes will significantly increase in response to OA.

4. Although recent studies suggest that calcification by some corals may be relatively tolerant of OA, this may provide little relief to coral reef ecosystems if bioerosion and CaCO_3 dissolution increase to the extent that reef erosion exceeds accretion. The condition when CaCO_3 loss exceeds gain represents a physical tipping point at which coral reefs can no longer be sustained, but the chemical threshold, timing, and rate of demise are poorly understood.
5. NEC is an instantaneous measurement of the balance between community gross calcification and dissolution and is a function of several parameters, including community composition, light, temperature, food and nutrients, hydrographic regime, and seawater CO_2 chemistry (e.g., CO_2 , H^+ , HCO_3^- , CO_3^{2-} , and CaCO_3 saturation state). Hence, NEC varies significantly over time and between different habitats and locations.
6. Using relationships between NEC and Ω_a derived from natural diel and seasonal cycles to predict future effects of OA on coral reefs must be done with caution. These relationships do not necessarily represent functional relationships between NEC and Ω_a , and more likely represent the rate of NEC as a function of the net effect of total reef metabolism on seawater Ω_a . NEC rates would prove more interpretable if NEP—which strongly impacts the local DIC:TA ratios and hence Ω_a —were considered.
7. Because of the strong coupling between the dominant biogeochemical processes on coral reefs (i.e., photosynthesis and calcification, respiration and dissolution) and their effect on seawater CO_2 chemistry, the relationships between NEC and Ω_a should be evaluated in concert with changes in DIC:TA ratios. This would help to resolve some of the previous disparities between different investigations, and potentially offers a valuable biogeochemical monitoring tool for tracking the long-term effects of OA and climate change on coral reef performance and function.

FUTURE ISSUES

1. What are the magnitudes of gross calcification and gross dissolution on coral reefs? Current estimates represent mainly the net of these processes.
2. What are the relative contributions of bioerosion and metabolic dissolution processes to the total gross dissolution on coral reefs? What proportion of bioeroded CaCO_3 material is actually dissolved? Where and when does most of the CaCO_3 dissolution occur?
3. How are major bioeroders, bioerosion rates, and metabolic dissolution rates affected by OA and climate change?
4. How do net CaCO_3 sediment dissolution rates in coral reef sediments vary in response to water column OA? How do sediment properties such as pore water chemistry, organic matter content, grain size, mineral composition, and advection influence net CaCO_3 sediment dissolution rates?
5. What are the in situ solubility and kinetics of biogenic CaCO_3 mineral phases, especially Mg calcite phases of varying Mg composition? How do reaction rates change as a function of OA and climate change?



6. What are the major controls of NEC and what is the functional dependence of NEC on seawater Ω_a ? Is decreasing NEC as a function of OA due to a decrease in calcification, an increase in dissolution, or a combination of both?
7. How will seawater Ω_a on coral reefs change in response to OA given that the benthic community exerts a strong control on the seawater chemistry? At what Ω_a will a given coral reef system undergo net dissolution, and what does this mean for the eco-services it provides? What is the rate of demise?

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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